Dispersal of Stable Flies (Diptera: Muscidae) From Larval Development Sites in a Nebraska Landscape

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ABSTRACT   Seven mark-recapture studies were conducted over 3 yr to assess dispersal of newly emerging adult stable flies, *Stomoxys calcitrans* L., from larval development sites in a mixed agricultural environment in northeastern Nebraska. Infested hay debris piles were marked by dusting their surfaces with fluorescent pigments, adults were captured with surrounding grids of Alsynite sticky traps, and specimens were dissected to determine feeding histories and reproductive age. Distances and directions of 3,889 marked specimens indicated males and females dispersed equally and in all directions. Midguts of males and females were equally likely to contain blood-meal remnants. Percentage with blood remnants and percentage of females with yolk increased with distance from mark origin, indicating survival and spread were positively associated with host finding success. A time-integrated diffusion model fit to results from the seven studies indicated 50% of stable fly adults had dispersed beyond 1.6 km of their natal site, but only 5% had dispersed beyond 5.1 km. These results indicate that stable fly adults on cattle in a given area are most likely to have originated from larval development sites within an ≈5 km radius of the subject cattle.

KEY WORDS   *Stomoxys*, dispersal kernel, diffusion model

Stable flies, *Stomoxys calcitrans* L. (Diptera: Muscidae), are serious blood-feeding pests of livestock in most parts of the world. Their economic impact to U.S. beef and dairy producers is estimated to exceed $1 billion (Taylor and Berkebile 2006). Bites by this fly cause stress and avoidance behaviors that reduce weight gains of pastured beef cattle (Campbell et al. 2001), growth and feed conversion rates of feedlot cattle (Campbell et al. 1987, Catangui et al. 1997), and lactation rates of dairy cattle (Bruce and Decker 1958). Stable fly larvae develop in decomposing vegetative materials, especially those contaminated with livestock manure and urine (Skoda and Thomas 1993).

Contaminated residues at sites where large round hay bales are fed to cattle during winter may be primary sources of early summer stable flies in grazing lands in the central United States (Broce et al. 2005, Talley et al. 2009), and these debris sites may be foci for spread of stable flies into neighboring landscapes.

In several reports, outbreaks of stable flies were observed in places where larval developmental sites were absent, and those observations prompted speculation that the outbreaks were the result of weather-assisted dispersal from more distant sources (Broce 1993; Jones et al. 1998, 1999).

Movement of stable flies in agricultural landscapes is not well characterized. Laboratory studies with flight treadmills indicate stable flies are capable of flying up to 29 km in 24 h (Bailey et al. 1973). Stable flies were observed to disperse 8 km in <2 h in south-central Oregon (Eddy et al. 1962) and up to 225 km over several days in the Florida panhandle (Hogsette and Ruff 1985). Gersabeck and Merritt (1985) found that 50% of flies released on Mackinac Island, MI, were recaptured within 0.45 km, and 90% were recaptured within 1.65 km. Flies released close to horses dispersed less than those released further away, and none of the released flies were collected on the Michigan mainland, ≈11 km away. Todd (1964) found that dairies adjacent to fly development sites in New Zealand were heavily infested, whereas stable flies were "no problem" within 1.6 km from developmental sites. The purpose of this study was to develop a mathematical model for dispersal of stable flies by studying spread of adults emanating from larval development sites in a mixed agriculture environment in eastern Nebraska. The resulting model will be useful to estimate distance of dispersal of adult flies from foci of larval development.

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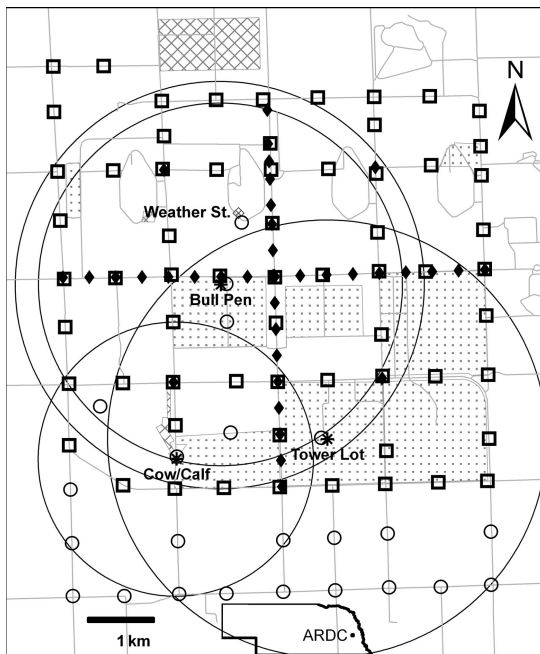
Fig. 1. Map of the University of Nebraska, Agricultural Research and Development Center, Ithaca, NE (ARDC). Solid diamonds indicate 2002 trap locations (diamond at the intersection represents four traps, one on each corner), open squares indicate 2004 and 2005 trap locations, and open circles indicate traps used only in 2005. Asterisks indicate marking sites. Circles surrounding marking sites represent the outer margins of the symmetrical trap arrays used to determine directionality of dispersal (Fig. 3). For BP, the inner circle represents 2002 and the outer circle representes 2004–2005. Diagonal cross-hatching indicates confined livestock facilities and stippling indicates pasture. Most of the remaining land was used for crop production.

Materials and Methods

Study Area and Design. Mark-recapture studies were conducted during 3 yr at the University of Nebraska, Agricultural Research and Development Center (ARDC), located near Ithaca, NE. The center encompassed a dairy, a feedlot, and ≈4,000 ha of fields devoted to crop production and pastures for beef cattle grazing (Fig. 1). Land use and management practices at the ARDC are representative of the central Great Plains. In winters between grazing seasons, the resident cow-calf herd was routinely fed hay from round bale feeders. This practice produced feed debris piles that consistently became stable fly developmental sites when weather warmed each year. Adult emergence from these sites peaked in mid-June and declined to low levels by early July (Taylor et al. 2007). Timing of this study was designed to coincide with peak stable fly emergence each year.

The overall goal of this study was to test and quantify the hypothesis that stable fly adults spread by simple diffusion from larval foci into the surrounding landscape. The study was patterned after the mark-recapture design and analysis used by Turchin and

Thoeny (1993) to study dispersal by southern pine beetle. In June 2002, 2004, and 2005, we scouted the ARDC premises to locate infested hay debris piles. We dusted the most infested ones with unique colors of DayGlo fluorescent pigment (DayGlo Color, Cleveland, OH) to mark adult flies that contacted the piles, either as they emerged from or visited the sites. At the same time, we deployed sticky traps in transects or grids around the piles to assess density-distance patterns of marked flies during the next 7–11 d.

Marking and Traps. We began in 2002 by marking two adjacent debris piles at one feeding location in a low-density cattle pasture (Fig. 1, Bull Pen [BP]). Corona Magenta (A-21) pigment was applied by hand at a rate of 1 kg/250 m^2 of pile surface between 0900 and 1000 hours on 21 June.

Sticky traps were 30-cm-diameter and 30-cm-tall cylinders of Alsynite fiberglass (Broce 1988) staked with tops at 1 m above ground in sunny locations. Traps were covered with 10 mil Sur-Flex plastic sleeves (Flex-o-glass, Chicago, IL) and coated with Tangle-Trap (The Tanglefoot Co., Grand Rapids, MI) diluted 1:1 with low odor paint thinner (Sunnyside, Wheeling, IL).

Traps were positioned at 0.4-km intervals along two perpendicular roadways that intersected 0.1 km N and 0.8 km E of the marked piles (Fig. 1). Additional traps were placed at four points in each diagonal direction, 2.25 km from the intersection, for a total of 39 locations. The Universal Transverse Mercator (UTM) coordinates (zone 14 N) of pile and trap locations were determined with ArcGIS 9.1 (ESRI, Redlands, CA). Traps were initially armed between 0500 and 0600 hours on 18 June and were serviced daily by 0800 hours through 28 June. Because stable flies are not active in darkness, flies on traps in a given morning were assumed to have been captured the previous day. Thus, from mornings of 18 June through 28 June, there were 3 trapping d before and 7 d after pigment was applied to piles.

In 2004, piles at three locations were marked simultaneously between 0900 and 1000 hours on 14 June (Fig. 1). Two adjacent piles were in the same BP pasture as was used in 2002 and were dusted with Arc Yellow (A-16N). A second cluster of three piles in the Tower Lot (TL) pasture was marked with Corona Magenta, and a third single pile in the Cow/Calf (CC) pasture was marked with Horizon Blue (T-19). The BP and TL piles were in pastures sparsely populated with cattle, whereas the CC pile was 50 m southeast of a feedlot containing ≈500 beef cattle.

Sticky traps in 2004 were arranged in a grid at 0.8-km intervals along section roads within ARDC (Fig. 1). Additional traps were placed in the middle of accessible sections to form an irregular grid of 67 traps asymmetrically surrounding the three marked piles. Pile and trap coordinates (±5 m) were determined with a Garmin eTrex Legend GPS unit (Garmin International, Olathe, KS). All traps were armed just before the piles were marked, and trapping continued until the morning of 24 June, for a total of 10 d after the piles were marked.

In 2005, piles in the same three locations were marked again, but with Horizon Blue at BP, Arc Yellow at TL, and Corona Magenta at CC. The trap grid from 2004 was extended an additional 1.6 km to the south to increase symmetry around the piles at TL and CC. Because few flies were captured from TL and CC in 2004, we placed one trap adjacent (<10 m) to each of the three marked piles to index abundance at the piles, for a total of 87 traps (Fig. 1). Traps were armed and piles marked by 1000 hours on 13 June, and trapping continued until the morning of 24 June, for a total of 11 d after marking.

Trap and Specimen Handling. In all 3 yr, traps were serviced daily by replacing sleeves and returning exposed ones to a field laboratory where they were examined under UV light (B100AP UV Lamp; UVP, Upland, CA). Nonmarked and marked stable flies were counted, and marked ones were removed for viewing and dissection under a stereoscope to determine their sex and physiological states, including prior feeding history and stage of gonotrophic development in females. Depending on year, up to 10 marked flies of each sex per trap-day were dissected to examine their digestive tracts at 12× for blood-meal remnants. Females were rated for gonotrophic age, as judged from evidence of yolk deposition in proximal oocytes viewed at 25×. Previtellogenic females had not initiated yolk deposition (stages 0 or 1, Scholl 1980), whereas vitellogenic ones contained yolk.

Meteorological Data. Records of daily precipitation and hourly air temperature, wind direction, wind speed, humidity, and radiation flux during the 3 study yr were obtained from the High Plains Regional Climate Center (University of Nebraska, Lincoln, NE) MEADTURFFARM station, located approximately in the center of the ARDC property (41.17° N, 96.47° W; Fig. 1).

Abundance of Nonmarked and Marked Flies of Different Kinds. Counts (c) of nonmarked and marked flies of each color from each trap and day were transformed as $z = \ln(c + 1)$ and averaged over traps within days to quantify daily catch rates of nonmarked and differently marked flies. We examined patterns in catch rates across days by comparing mean log catch rates of flies with different marks (from different sources, including none) and days in each year separately, treating marks and days as categorical main effects. Of particular interest was the significance of any interaction between source of mark and day. Interaction would be expected if catch rates of nonmarked flies were to remain steady, whereas concurrent catch rates of marked flies were to rise and decline differentially with time after dusts were applied and marked flies disappeared from the landscape.

Drift and Direction of Dispersal. Distributions of marked flies were analyzed for evidence that centers of flies dispersing from their respective piles differed among years and piles of origin. We calculated each marked specimen's northing (north-south displacement) and easting (east-west displacement) using UTM coordinates of the pile where marked and trap

Table 1. Radii of symmetrical circles surrounding sources for each year with the no. of traps used and marked stable flies collected to evaluate directionality of dispersal

Year	Site	Radius (km)	No. traps	Males	Females
2002	BP	2.77	31	277	297
2004	BP	3.12	36	129	87
2005	BP	3.12	45	729	496
2005	CC	2.10	22	264	171
2005	TL	3.35	49	764	449

where captured. To compensate for trap asymmetry, we confined this analysis to a subset of traps arranged around each source within the largest possible radius enclosing a symmetrical trap array (Table 1; Fig. 1). Flies from traps outside a pile's radius were disregarded.

Summary statistics for compiled northings and eastings were markedly non-normal, leptokurtotic, and skewed (data not shown), so we estimated centers (±95% confidence intervals) of observed northings and eastings with nonparametric bootstrap sampling (Davison and Hinkley 1997), using *boot* in *R* (*R* Development Core Team 2009) and 10,000 resamplings with replacement. Differential dispersal by males and females would be indicated if their respective confidence limits did not overlap. Drift from a given pile would be indicated if confidence limits were significantly different from zero (Turchin and Thoeny 1993).

Dispersal by Different Subcategories of Flies. We examined differences in dispersal distances among males and females from the different years and source piles and among flies differing in feeding history and vitellogenic status. To do this, we fit Poisson regression models to counts of marked flies grouped into consecutive distance annuli, with outer limits set at 0.5, 1.0, 2.0, and 6.75 km to assure flies were present in each annulus. This approach ignored direction and made no assumption about the shape of the underlying density-distance curve. Explanatory main effects were sex, index for distance annulus, and year, and interactions were all pairwise combinations of main effects. Primary interest was in significance of coefficients for interactions between sex and annulus and feeding history and annulus, which would indicate males and females or individuals of differing feeding histories had dispersed differentially.

A longitudinal analysis considered the subset of flies that had been marked at the BP pile in 2002, 2004, and 2005 to evaluate year-to-year variation in dispersal from that location. A second cross-classified analysis considered flies that had dispersed from each of the three sources in 2004 and again in 2005. Alternative models were fit with Proc GENMOD (SAS Institute 2004), magnitudes of effects of interest were judged from least-squares fitted means, and significance of coefficients was judged with χ^2 statistics for likelihood-ratio tests that coefficients differed from zero.

Density–Distance Relations. In a fourth set of analyses, we examined the relationship between catch rate

per day and matching radial distance from source, with the direction ignored. The hypothesis of simple diffusion predicts that catch rate would decline with distance from source of mark. However, rate of decline could vary among days after flies were marked at a given pile, and rate of decline could vary with source, depending on features of the landscape that could affect dispersal and apparent survival of marked flies.

We first used an empirical regression model to examine rates of decline in daily catch rate with days after marking and distance from source. We analyzed data from the four subsets with greatest numbers of flies caught, namely from BP in 2002, 2004, and 2005 and TL in 2005. For each subset, we calculated radial distance to each trap as $r = \sqrt{x^2 + y^2}$, where x and y were the trap's easting and northing from source pile, respectively. Traps around each source were grouped into mutually exclusive annuli with outer limits of 0.25, 1, 2, 3, 4, 5, 6, and >6 km, and mean radial distances ($\bar{r}$) were calculated for traps in each annulus. Corresponding counts (c) of flies with marks from each trap on each day were averaged, and the averages by annulus and day were analyzed in relation to distance using a simple empirical model,

$$\ln(\bar{c} + k) = a + b\sqrt{\bar{r}}$$

The small number k ($=1/$[no. traps per annulus]) overcame cases where mean daily catch rates in some annuli were zero. Transformations of both catch rates and distances overcame nonlinearity and unequal variances in residuals over the range of r. Transformations also prevented exceptionally large catch rates at traps close to sources from dominating the analysis (Turchin and Thoeny 1993). Slopes (b) over distances out to 3 km were calculated for each source and day, and slopes were analyzed with analysis of covariance (ANCOVA) over consecutive days after marking, grouped by set. Residuals were examined graphically for constant variance and normality.

Because results from the empirical regressions indicated patterns of dispersion around each source pile were stable among days and piles, we proceeded to model dispersal as a simple diffusion process. Our field methods produced what Turchin (1998) referred to as "time-integrated density data." Rather than being quasi-instantaneous events, timing of marking and subsequent captures were distributed over consecutive days. Turchin and Thoeny (1993) showed that, with time-integrated data, cumulative catch rate would be related to distance as

$$C_r = Ar^{-1/2}\exp(-r/B),$$

where C_r is daily catch rate at a given trap location (total number caught divided by number of trapping days in the study), and r is as above. The term A defines the height of the dispersal curve and is jointly proportional to number of marked specimens released and to capture efficiency of traps. The term B defines the width of the curve and is proportional to rate of spread and inversely proportional to per capita loss rate through death, exit from the study area, or transition into a behavioral state, life stage, or microhabitat

Table 2. Average daily (range) temperatures, wind speeds, and total precipitation recorded at the MEADTURFFARM weather station during the three experimental periods

Year	Daily extreme temperatures (°C)		Wind speed[a] (km/h)	Total precipitation (cm)
	Minimum	Maximum		
2002	20.1 (18–23)	34.4 (32–36)	8.8 (6–12)	0
2004	13.8 (9–18)	24.7 (18–28)	9.2 (6–13)	0.50
2005	16.8 (12–22)	30.2 (26–34)	13.4 (8–21)	0.03

[a] Daytime hours, 0900–1700 hours.

that renders marked individuals unavailable or unresponsive to traps. Because variances in residuals were not constant, we followed the recommendation of Turchin and Thoeny (1993) to combine the catch rates and distances into annuli and analyze them as

$$\ln(\bar{C}_{\bar{r}} + 1/2\ln(\bar{r}) = \ln(A) - \bar{r}/B,$$

where $\bar{C}_{\bar{r}}$ is mean catch rate per day and $\bar{r}$ is corresponding mean radial distance. Data from each marking site and year were analyzed separately, and slopes among sites and years were compared with ANCOVA. Residuals were examined to assess consistency with the model, with special attention given to adequacy of fit at the outer, right end "tails" of the curves.

Projected Dispersal Distances. Turchin and Thoeny (1993) showed that r_p, the radius of a circle enclosing an arbitrary proportion p of dispersers, can be estimated from

$$p = \frac{\displaystyle\int_0^{r_p} r^{1/2} \exp[-r/B]dr}{\displaystyle\int_0^{\infty} r^{1/2} \exp[-r/B]dr}$$

To determine dispersal radii for different values of B, we set values of p at 0.5, 0.67, 0.95, and 0.99 and solved iteratively for r_p, using QuickMath's implementation of Mathematica (http://www.quickmath.com/).

Results

Weather during the trapping intervals in the 3 yr was generally favorable for stable fly flight and trapping (Table 2). Temperatures were warmest in 2002, coolest in 2004, and intermediate in 2005. Daily minimum temperatures exceeded 9°C on all days. No precipitation occurred in 2002, and little occurred in 2004 and 2005. Hourly daytime winds between 0900 and 1700 hours ranged from 6 to 21 km/h, averaged 9–13 km/h, and were variable in direction over the 3 yr.

Totals of 133,564 nonmarked flies and 3,889 marked flies were obtained with 1,900 d of trap effort during the 3 yr (Table 3). All marked flies were dusted with

Table 3. Details of dispersal studies and numbers of nonmarked and marked adult stable flies caught on sticky traps

Year	Number			No. not marked	No. marked[b]			
	Traps	Days	Trap-days[a]		BP	CC	TL	Total
2002	39	7	273	28,149	578	—[c]	—[c]	578
2004	67	10	670	51,634	224	21	31	276
2005	87	11	957	53,781	1,260	449	1,326	3,035
Total		28	1,900	133,564	2,062	470	1,357	3,889

[a] No. trap-days.
[b] Sources of marks were feed debris piles in Bull pen (BP), Cow-calf (CC), or Tower lot (TL) pastures (see Fig. 1).
[c] Piles in CC and TL were not marked in 2002.

a single color from a single source pile, except for one female in 2005, which occurred on the trap adjacent to the BP site. That female was dusted with two colors—one from BP and the other from TL. This doubly marked fly was disregarded from further analysis.

Abundance of Nonmarked and Marked Flies of Different Kinds. Numbers of trapped flies varied substantially among years and sources (Table 3). Among the three marking sites, numbers from the cow/calf (CC) site were consistently lower than from the other two sites. The number from TL was low in 2004 but higher and similar to numbers from BP in 2005. Differences in numbers caught with the different marks may have been a result of differences in numbers naturally emerging from the marked piles, but numbers that actually emerged were not estimated (but see below).

Geometric mean daily catch rates of nonmarked flies averaged 41, 54, and 31 flies per trap-day among 2002, 2004, and 2005, respectively (Fig. 2). Within each year, catch rates of nonmarked flies were reasonably stable over consecutive days, except for a striking decline during 18 June 2004, which coincided with a passing cold front. Mean air temperature from 0800–1800 hours on that date was 15.5°C, which was >5°C cooler than during the 2 adjacent d.

Matching catch rates of marked flies from the different sources were much lower, increased when dusts were applied to piles, and declined thereafter (Fig. 2). Analysis of variance (ANOVA) indicated that patterns of abundance of nonmarked and marked specimens from 21 through 27 June 2002 were significantly different (color-day interaction, $F = 2.36$; df = 6,502; $P < 0.03$). Parallel analyses for 2004 and 2005 also indicated that patterns in abundance of nonmarked and marked flies were dissimilar (2004: $F = 30.0$; df = 27,2640; $P < 0.01$. 2005: $F = 4.45$; df = 30,3784; $P < 0.01$). These results indicated dusting of source piles succeeded in marking cohorts of flies that emerged and dispersed from their natal piles and subsequently disappeared for the most part during the 7- to 11-d intervals after dusts were applied.

Direction and Distance of Dispersal. Very few flies were recaptured from TL and CC in 2004 (Table 3), so we placed one additional trap adjacent to each of the three marking sites in 2005 to index numbers marked at each site. Similar numbers were obtained at those individual traps in 2005: 413 at BP, 624 at TL, and 424 at CC. In contrast, widely different numbers of marked flies from the same sites were obtained on traps in the surrounding landscape: 847 from BP, 702 from TL, but only 25 flies from CC. Compared with BP and TL, flies marked at CC were much less likely to have been trapped in the surrounding landscape. Locations of 3,663 marked males and females, grouped by source pile and year, were analyzed for evidence that spread from source piles was directional (Table 1). Totals of 21 and 31 flies, marked in 2004 at CC and TL, respectively, were too few to analyze. Also, 47 flies from BP in 2002, 2004, and 2005, 113 from TL in 2005, and 14 from CC in 2005 were disregarded because they were from traps outside their piles' respective radii of symmetrical traps (Fig. 1). Confidence intervals for centers of matching males and females from each source and year overlapped substantially, which indicated males and females had dispersed equally and in the same directions (data not shown).
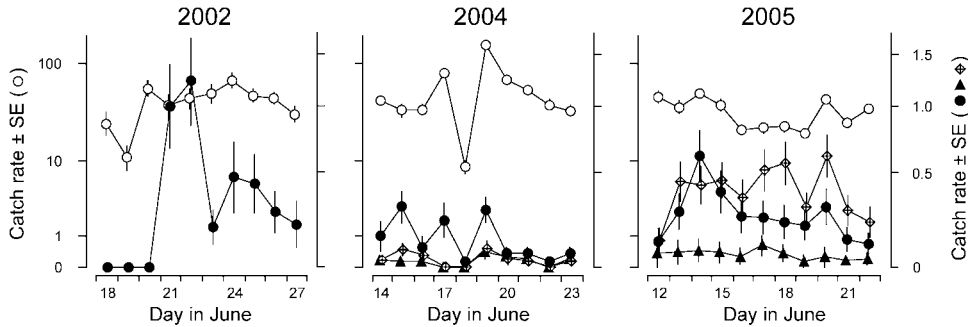

Fig. 2. Abundance of nonmarked and marked stable flies on sticky traps during study periods. Open circles are for nonmarked flies and filled circles, triangles, and diamonds are for flies marked at debris piles in the bull pen, cow-calf lot, and tower lot, respectively.
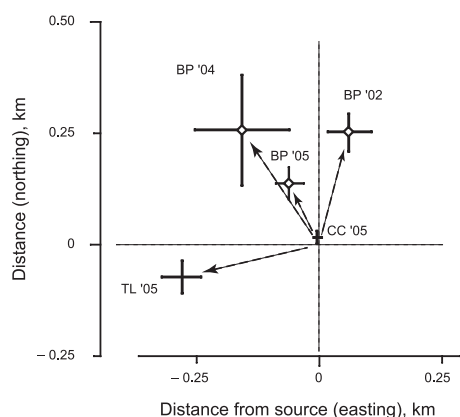
Fig. 3. Centers and 95% bootstrap confidence limits for mean northings and eastings of marked stable flies from traps centered around marked source piles.
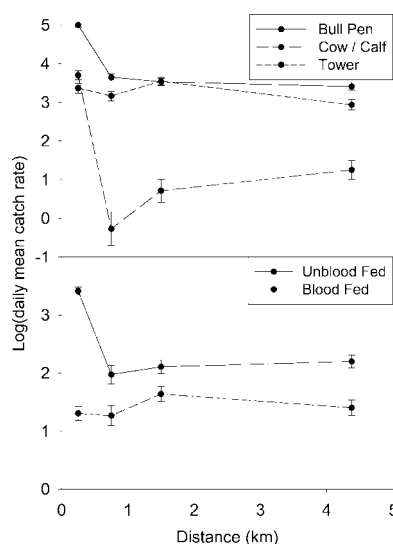

Fig. 4. Least-squares estimates of numbers of stable flies with increasing distance from marking sites, 2004 and 2005 combined. (Top) Numbers from different sources, sexes combined. (Bottom) Numbers with and without blood-meal remnants, sexes, and marking sites combined.

Sexes combined, centers of the dispersed flies were significantly displaced from their respective source piles in four of the five cases (Fig. 3). Centers from BP in 2002, BP in 2004, BP in 2005, and TL in 2005 were all significantly different from origins, whereas the center of flies from CC in 2005 was not different. However, distances from origins ranged from a maximum of 0.3 km WSW from TL in 2005 to a minimum of 0.014 km NW of CC in the same year. Directions of centers among years were not positively correlated with matching daytime wind directions in individual years. Also, centers of the three cohorts in 2005 that dispersed at the same time from their respective sources were significantly different from each other. Clearly, drift of each cohort from its respective source was trivial in magnitude, and directions of drift were independent of concurrent wind directions.

Dispersal by Different Categories of Flies. Counts of marked female and male stable flies changed with increasing distance between traps and sources of marks. Among flies marked at BP in 2002–2005, counts were always greatest on traps in the annulus nearest the marking piles, but patterns among progressively more distant annuli varied among years (data not shown) (year $\times$ distance interaction, $\chi^2 = 98.3$, df $= 6$, $P < 0.01$). Similarly, counts declined differently with distance from BP, CC, and TL in 2004 and 2005 (source $\times$ distance, $\chi^2 = 582$, df $= 6$, $P < 0.01$; Fig. 4, top). Compared with catch rates on traps within 0.5 km of the flies' respective sources, catch rates around BP in both years declined steadily with distance, they remained relatively stable around TL, but they dipped sharply within 0.5–2 km of CC, and then returned to greater levels at distances beyond 2 km.

Relative frequencies of female and male stable flies did not differ with distance from marking sites. Females represented 41–52% of flies marked at BP over 2002–2005, and differences among years were significant (years: $\chi^2 = 18.0$, df $= 2$, $P < 0.01$; Table 4). However, relative frequencies within each year were similar among the four distance annuli (sex $\times$ distance, $\chi^2 = 4.82$, df $= 3$, $P = 0.185$). In 2004 and 2005,

females were also underrepresented, but less variably among flies marked at the BP, CC, and TL sites (sex $\times$ source: $\chi^2 = 2.24$, df $= 2$, $P = 0.33$), over the 2 yr (sex $\times$ year: $\chi^2 = 0.35$, df $= 1$, $P = 0.54$), and among distance annuli (sex $\times$ distance: $\chi^2 = 0.30$, df $= 3$, $P = 0.96$). Deficit of females was most likely caused by differences in trapability of the two sexes with Alsynite sticky traps. Absence of interactions with distance indicated males and females dispersed similarly from the different sites over the 3 yr.

Dissections of males and females indicated $\approx$23% of the marked flies from all years and sources had blood-meal remnants in their guts (Table 4), but frequencies with remnants changed differentially with distance. Among flies from BP in 2002–2005, numbers of specimens without remnants were greatest nearest their source, but decreased to steady levels with increasing distance (data not shown). In contrast, abundance of flies with remnants remained steady or increased slightly. Thus, only 7% of flies within 0.5 km had remnants, whereas 20–25% did so further out from their source (remnant $\times$ distance: $\chi^2 = 64.7$, df $= 3$, $P < 0.01$). A parallel pattern occurred with flies marked at the three sources in 2004–2005 (Fig. 4, bottom; remnant $\times$ distance: $\chi^2 = 132.2$, df $= 3$, $P < 0.01$). In both analyses, flies trapped within 0.5 km of the source of their mark were least likely to have blood-meal remnants; however, percentage with remnants was higher but otherwise stable with increasing distance. Male and female flies were equally likely to contain blood-meal remnants in both BP in 2002–2005 (sex $\times$ remnant: $\chi^2 = 0.06$, df $= 1$, $P = 0.8$) and BP, CC, and TL in 2004 and 2005 (sex $\times$ remnant: $\chi^2 = 2.8$, df $= 1$, $P = 0.09$).

Dissections of females showed an average of 11% were vitellogenic overall (Table 4). Frequencies

Table 4. Numbers of marked male and female stable flies from different sources and years, percentages of dissected ones that had remnants of a blood meal in their guts, and percentages of females with yolk in their ovarioles, by source of mark and year of capture

Origin of mark	Year	Males		Females		
		n	Fed (%)	n	Fed (%)	Yolk (%)
Bull pen (BP)	2002	280	8.7	298	5.8	8.2
	2004	131	22.9	93	10.9	3.3
	2005	750	20.4	510	21.7	10.0
Cow/calf (CC)	2004	10	60.0	11	27.3	9.1
	2005	271	16.1	178	11.0	4.2
Tower lot (TL)	2004	19	52.6	12	60.0	30.0
	2005	826	28.4	500	34.0	16.4
	Combined	2,287	23.0	1,602	22.4	11.3

among females from BP in 2002–2005 did not differ with distance from origin (yolk × distance: $\chi^2 = 7.02$, df = 3, $P = 0.07$). Frequencies among females from the three sources in 2004 and 2005 did differ with distance (yolk × distance: $\chi^2 = 9.2$, df = 3, $P = 0.033$); compared with 9–11% on traps <1 km from their sources, 16% were vitellogenic at 1–2 km, and 23% were vitellogenic at more distant trap locations.

Finally, frequencies of vitellogenesis and blood-meal remnants among females were positively associated among flies from BP over the 3 yr (blood × yolk: $\chi^2 = 36.3$, df = 1, $P < 0.01$) and from all three sites in 2004 and 2005 (blood × yolk: $\chi^2 = 92.4$, df = 1, $P < 0.01$). Dispersal distances, host finding, and vitellogenesis were all positively associated with each other; the further a female was captured from its marking source, the greater the chance it contained blood-meal remnants and was vitellogenic.

Density–Distance Curves. Spatial patterns in catch rates among traps surrounding the BP piles in 2002–2005 and TL in 2005 indicated stable flies dispersed rapidly into the surrounding landscapes the day each pile was marked (Fig. 5). Slopes of catch rates versus trap distances on those first days were significantly negative in all five cases (Student's t-test < −4.7, df = 2 each, $P < 0.04$) and consistent among piles (source × distance interaction: $F = 0.26$; df = 3,8; $P = 0.85$). Furthermore, slopes over succeeding days for each pile remained statistically the same (day × distance interactions: maximum $F = 2.60$; df = 5–9,11–20; $P > 0.12$).

Turchin's time-integrated diffusion model (eqn. 4) conformed reasonably well with the pattern of decline in catch rates with radial distance from the different source piles in the different years (Fig. 6). Fitted values for the vertical scale factor, A, varied from <1 to >10, which we attribute to natural differences in numbers of flies emerging from the different source piles. Estimates of the horizontal dispersal parameter, B, ranged from 0.73 to 3.09. However, ANCOVA indicated that the variance in B was not significant among the seven studies ($F = 1.30$; df = 6,30; $P = 0.29$). In turn, we refitted the model to all results combined, and obtained a pooled estimate of $A = 3.91 \pm 1.99$ (SE) and $B = 1.31 \pm 0.23$ ($R^2 = 0.92$). Residuals from the pooled regression were independent of fitted means ($r = 0.60$, $P = 0.11$), but residuals at the right end of each curve were above the fitted lines in all cases,

suggesting some of the marked flies were dispersing farther than would be predicted by simple diffusion with loss from their respective sources.

Projected Dispersal Distances. We used the pooled estimate of $B \pm 95\%$ CL to calculate radii of circles enclosing 50, 67, 95, and 99% of stable flies dispersing
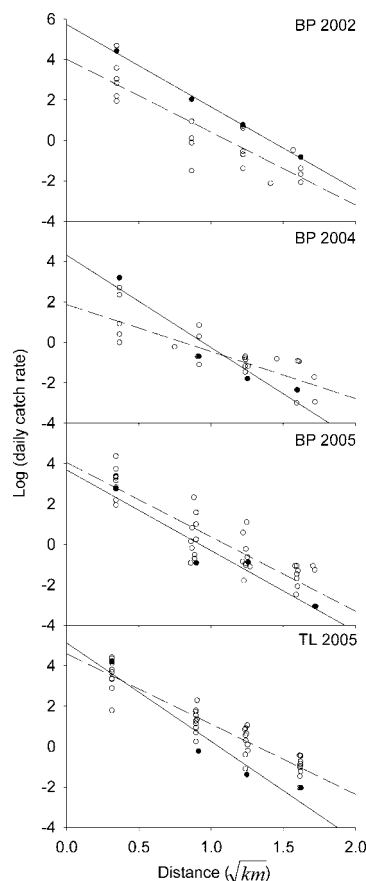

Fig. 5. Catch rates of marked stable flies over increasing distances from marked debris piles BP 2002–2005 and TL 2005. Points are average catch rates per day (log scale) and matching mean distances (square root scale) for traps grouped in concentric annuli out to 3 km. Filled circles and solid lines are day 1, when source piles were marked. Open circles and dashed lines are subsequent days superimposed. Lines are least-squares regression lines.
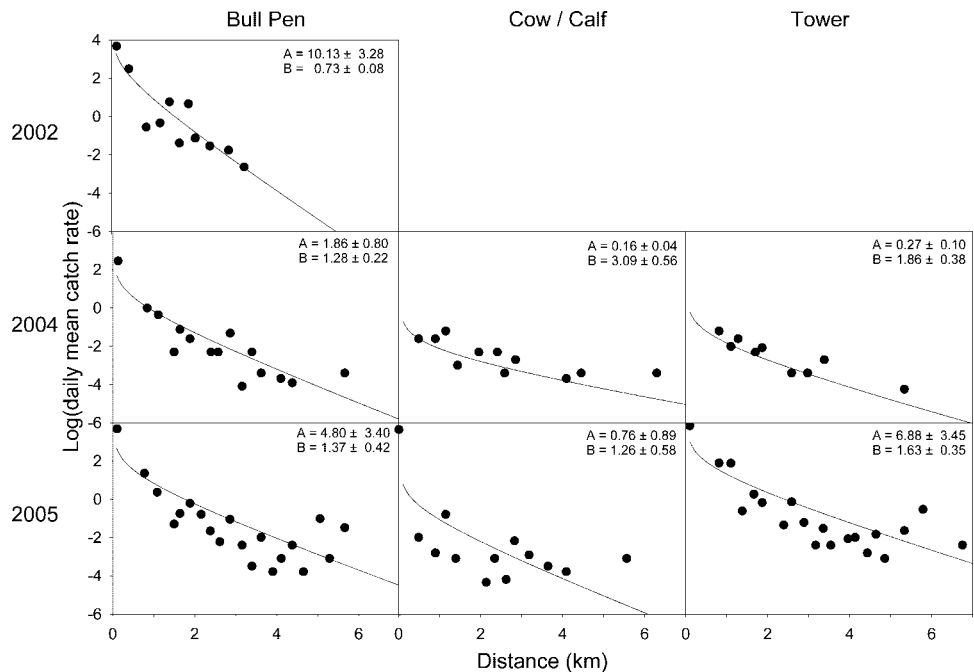
Fig. 6. Daily catch rates of marked stable flies at increasing distances from marking sites. Points are natural logs of arithmetic mean catch rates and averaged distances on traps within concentric radii from sources of marks. Lines are fitted time-integrated diffusion curves (eq. 4), with values of A and B ($\pm$SE) as designated.

from a hypothetical larval developmental site (Table 5). Using mean value for B, 50% of dispersing flies were predicted to remain within 1.6 km of their natal site, and 95% were predicted to remain within 5.1 km.

Discussion

The number of naturally marked stable flies captured during this 3-yr study was a substantial 3,889 specimens, much greater than the 59 specimens recaptured by Bailey et al. (1973), but similar to the 3,535 flies recaptured by Gersabeck and Merritt (1985). Although we were unable to estimate the numbers of flies that were actually marked at each of the seven marking sites, our techniques succeeded in marking and capturing enough specimens on transects or grids of Alsynite sticky traps to analyze dispersal distances on a daily basis around four of the seven sites and on a cumulative basis over 7–11 d around all seven sites.

Table 5. Estimated radii enclosing arbitrarily designated proportions of stable flies dispersing from point sources into the surrounding landscape, based on extrapolation of fitted time-integrated diffusion model, with confidence interval based on corresponding limits for spread parameter B (Fig. 6)

Proportion enclosed	Radius (km)	95% limits (km)	
		Lower	Upper
0.50	1.55	0.88	2.22
0.67	2.20	1.25	3.14
0.95	5.12	2.92	7.32
0.99	7.43	4.23	10.62

The marked specimens were wild flies that had developed in the field naturally rather than under artificial laboratory conditions. Furthermore, their dispersal was observed in a natural landscape containing a mix of cultivated crops, occupied cattle pastures, and livestock confinement facilities much like most of the central United States.

Results of dissections indicated that the marked flies that we captured were relatively young specimens that had recently emerged from their natal origins. Frequencies of blood-meal remnants were generally <25% in both males and females and were lowest among traps within 0.5 km of the marking sites (Fig. 4, bottom). Also, rates of vitellogenesis were <12% everywhere and were also lowest near source piles. These findings are most consistent with the hypothesis that the marked flies acquired their marks as they emerged from the dusted piles rather than having emerged elsewhere and acquired marks while visiting the marked piles as fed, reproductively older specimens.

Patterns of abundance of marked flies around the BP and TL sites in 2003–2005 were most consistent with simple, omnidirectional diffusion. Centers of trapped males and females were indistinguishable and were displaced by <0.3 km from corresponding origins. The landscapes surrounding these sites were sparsely populated with cattle. In contrast, flies marked at CC in 2005 appeared to be much more sedentary (Fig. 6), and catch rates of flies from that site were generally lower than from the other sites. It

is plausible that flies that emerged from the CC site aggregated in the adjacent 500-head feedlot. Unfortunately, none of our traps were placed within that feedlot, so we are unable to address this issue further. It is notable that, when Gersabeck and Merritt (1985) released marked flies near large numbers of horses, those flies dispersed shorter distances than counterparts released where there were fewer horses. In New Zealand, Todd (1964) concluded that few flies dispersed farther than necessary to obtain bloodmeals. Bailey et al. (1973) indicated that flies tended to remain near hosts once located.

If marked flies at ARDC remained trappable and were living as long as our trapping intervals, simple diffusion predicts that density–distance curves around each source pile would have continued to shift outward with time after marking started. Contrary to that prediction, slopes of the density–distance curves were remarkably stable among consecutive days after marks were applied (Fig. 5), and very few marked flies were captured on the outermost traps beyond 3 km (data not shown). These findings suggest that emergence rates of young flies at the marking sites were counterbalanced by early mortality or rapid transition of those marked flies into a behavioral state that was unresponsive to Alsynite traps. Further study with complimentary fly collecting methods near and far from host animals will be needed to determine whether dispersal patterns of older flies vary from the ones observed in this study.

As first approximations, the time-integrated diffusion model of Turchin and Thoeny (1993) conformed reasonably well to the density-distance data surrounding each of our seven marking sites (Fig. 6). Exceptions were that catch rates nearest the sources and at distances beyond 5 km tended to be greater than predicted, possibly resulting in an underestimation for the outer radii. Gersabeck and Merritt (1985) observed that median dispersal ($=r_{0.5}$) was between 0.3 and 0.9 km. However, those authors reported that hosts were readily available near all of their release points, possibly reducing the dispersal distances of the stable flies in their study.

The dispersal distance observed in this study is less than the potential dispersal distances proposed by Bailey et al. (1973), based on flight mill studies, and much lower than the dispersal distances observed by Hogsette et al. (1987) on the Florida Gulf Coast. All of the long-range dispersing stable flies observed by Hogsette and Ruff (1985) were collected after the passage of a strong cold front downwind of strong north to northeastern winds. In addition, in the Florida study, the flies passed through a broad band referred to as the sand hill zone where potential hosts were sparse. Those situations differed greatly from conditions during our study in eastern Nebraska. Although moderate winds were observed during the study periods, they tended to be variable over the duration, centers of drift were independent of matching wind directions, and distances were trivial compared with concurrent wind runs. Results of our study indicate that the majority of the stable flies in a mixed agri-cultural environment disperse far less than the maxima indicated in earlier studies.

Our projected dispersal distances will be useful to livestock managers seeking to use source reduction as a strategy to reduce stable fly injury to livestock. For confined animals, efforts should be directed at potential larval development sites within and adjacent to the confinement facility. For grazing animals, sanitation should be directed at winter hay feeding sites in spring, before larval development can begin, and at summer feeding sites when supplementation is needed. For both confined and grazing animals, the dispersal radii estimated from our study indicate sanitation will need to be implemented within an ≈5-km radius.

References Cited

Bailey, D. L., T. L. Whitfield, and B. J. Smittle. 1973. Flight and dispersal of the stable fly. J. Econ. Entomol. 66: 410–411.

Broce, A. B. 1988. An improved alsynite trap for stable flies, *Stomoxys calcitrans* (Diptera: Muscidae). J. Med. Entomol. 25: 406–409.

Broce, A. B. 1993. Dispersal of house flies and stable flies, pp. 61–69. *In* G. D. Thomas and S. R. Skoda (eds.), Rural flies in the urban environment. North Central Regional Res. Publ. No. 335. University of Nebraska, Lincoln, NE.

Broce, A. B., J. Hogsette, and S. Paisley. 2005. Winter feeding sites of hay in round bales as major developmental sites of *Stomoxys calcitrans* (Diptera: Muscidae) in pastures in spring and summer. J. Econ. Entomol. 98: 2307–2312.

Bruce, W. N., and G. C. Decker. 1958. The relationship of stable fly abundance to milk production in dairy cattle. J. Econ. Entomol. 51: 269–274.

Campbell, J. B., I. L. Berry, D. J. Boxler, R. L. Davis, and D. C. Clanton. 1987. Effects of stable flies (Diptera: Muscidae) on weight gain and feed efficiency of feedlot cattle. J. Econ. Entomol. 80: 117–119.

Campbell, J. B., S. R. Skoda, D. R. Berkebile, D. J. Boxler, G. D. Thomas, D. C. Adams, and R. Davis. 2001. Effects of stable flies (Diptera: Muscidae) on weight gains of grazing yearling cattle. J. Econ. Entomol. 94: 780–783.

Catangui, M. A., J. B. Campbell, G. D. Thomas, and D. J. Boxler. 1997. Calculating economic injury levels for stable flies (Diptera: Muscidae) on feeder heifers. J. Econ. Entomol. 90: 6–10.

Davison, A. C., and D. V. Hinkley. 1997. Bootstrap methods and their application. Cambridge University Press, New York.

Eddy, G. W., A. R. Roth, and F. W. Plapp. 1962. Studies on the flight habits of some marked insects. J. Econ. Entomol. 55: 603–607.

Gersabeck, E. F., and R. W. Merritt. 1985. Dispersal of adult *Stomoxys calcitrans* (L.) (Diptera: Muscidae) from known immature developmental areas. J. Econ. Entomol. 78: 617–621.

Hogsette, J. A., and J. P. Ruff. 1985. Stable fly (Diptera: Muscidae) migration in northwest Florida. Environ. Entomol. 14: 170–175.

Hogsette, J. A., J. P. Ruff, and C. J. Jones. 1987. Stable fly biology and control in Northwest Florida. J. Agric. Entomol. 4: 1–11.

Jones, C. J., J. A. Hogsette, S. A. Isard, Yu-Jie Guo, G. Greene, and A. B. Broce. 1998. Using phenology to detect dispersal of stable flies in western Kansas, pp. 348–351. *In* Proceedings of the American Meteorological Society, 13th Conference on Biometeorology and Aerobiology. American Meteorological Society, 2–7 November 1998, Albuquerque, NM.

Jones, C. J., S. A. Isard, and M. R. Cortinas. 1999. Dispersal of synanthropic Diptera: lessons from the past and technology for the future. Ann. Entomol. Soc. Am. 92: 829–839.

R Development Core Team. 2009. R: a language and environment for statistical computing. (http://www.R-project.org).

SAS Institute. 2004. SAS 9.1.3 help and documentation. SAS Institute, Cary, NC.

Scholl, P. J. 1980. A technique for physiologically age-grading female stable flies, *Stomoxys calcitrans* (L.). Nebr. Agric. Exp. Stn. Res. Bull. Research Bulletin No. 298, Institute of Agriculture and Natural Resources, University of Nebraska, Lincoln, NE.

Skoda, S. R., and G. D. Thomas. 1993. Breeding sites of stable flies and house flies, pp. 61–69. *In* G. D. Thomas and S. R. Skoda (eds.), Rural flies in the urban environment. Research Bulletin No. 317, Institute of Agriculture and Natural Resources, University of Nebraska, Lincoln, NE.

Talley, J. L., A. B. Broce, and L. Zurek. 2009. Characterization of stable fly (Diptera: Muscidae) larval development habitat at round hay bale feeding sites. J. Med. Entomol. 46: 1310–1319.

Taylor, D. B., and D. R. Berkebile. 2006. Comparative efficiency of six stable fly (Diptera: Muscidae) traps. J. Econ. Entomol. 99: 1415–1419.

Taylor, D. B., D. R. Berkebile, and P. J. Scholl. 2007. Stable fly population dynamics in eastern Nebraska in relation to climatic variables. J. Med. Entomol. 44: 765–771.

Todd, D. H. 1964. The biting fly *Stomoxys calcitrans* (L.) in dairy herds in New Zealand. New Zeal. J. Agric. Res. 7: 60–79.

Turchin, P. 1998. Quantitative analysis of movement. Measuring and modeling population redistribution in animals and plants. Sinauer, Suderland, MA.

Turchin, P., and W. T. Thoeny. 1993. Quantifying dispersal of southern pine beetles with mark-recapture experiments and a diffusion model. Ecol. Appl. 3: 187–198.